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Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae)

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Observations on the mating systems of two spiders, *Linyphia hortensis* **Sund. and** *L. triangularis* **(Cl.) (Linyphiidae: Araneae). -** Observations on the phenology of the spiders, the operational sex ratio, precopulatory mate guarding and fighting behaviour are reported. Differences in the copulatory behaviour like remating probability of females and sperm priority patterns are discussed.

In both species males mature before the females and the operational sex ratios are male biased. Males guard subadult females until their final moult and defend them against intruders. Male fights in *L. triangularis* are longer, more intense and riskier than in *L. hortensis*. In *L. triangularis* receptive females are present only for a short period because most subadult females moult within a few days, copulating males seal the copulatory openings of the females with mating plugs and remating probability of females in the laboratory is very low. In *L. hortensis* receptive females are to be found during a prolonged period since they are less well synchronized in their final moult, they may copulate more than once and second males can fertilize a small portion of the females eggs. Therefore copulations with virgin females are probably more valuable to *L. triangularis* males than to *L. hortensis* males. Because males should adjust their investment of energy and time into fights according to the expected gains the differences in the mating patterns and the availability of receptive females are probably responsible for the observed differences in the fighting behaviour of the males of the two species.

Key-words: mating systems - Linyphiidae - phenology - mate guarding - fighting behaviour - remating probability

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INTRODUCTION

The mating system (or mating pattern) of a species can be defined as the relationships and interactions between females and males in the context of reproductive behaviour. It comprises a specific set of behavioural mechanisms and adaptations which have evolved under the influence of the often conflicting reproductive interests of the two sexes and species-specific or population-specific ecological constraints.

In this paper a short summary will be given of the mating systems of two closely related species of linyphiid spiders, *Linyphia hortensis* and *L. triangularis*. We focus here only on a few important factors which shape and characterize the mating systems with our main interest directed to the intensity of intrasexual competition in males. The factors considered here are as follows: (1) the temporal availability of mates, (2) the behavioural mechanisms males use to optimize their reproductive success and (3) the females' remating behaviour.

Therefore we will present data on the phenology of the two *Linyphia*-species (length and timing of male and female moulting periods), the operational sex ratio (i.e. the ratio of receptive females to sexually active males at any given time, EMLEN & ORING 1977), the guarding and fighting behaviour of the males and the remating probability of the females. Common features of the two mating systems and differences between them will be outlined and possible behavioural consequences will be discussed.

NATURAL HISTORY OF THE SPECIES

Both *Linyphia* species are very common and widespread in Europe, *L. hortensis* prefers shady habitats like woods and hedges, whereas *L. triangularis* lives in almost any location where a shrub layer is present. Webs of both species are mostly located in the upper part of the herb layer, *L. triangularis* webs can also be found in the lower parts of the shrub layer. The webs are typical sheet webs with a horizontally oriented web sheet and irregular mesh-works of threads above and below this sheet. The species have an annual life cycle with a rather short reproductive period: *L. hortensis* reproduces in spring and early summer (April to June), whereas the reproductive period of *L. triangularis* is in summer and fall (July–September).

METHODS

Investigations were carried out between 1987 and 1993. Data from several years were pooled if there were no significant differences between years. Field observations were made in appropriate habitats near Würzburg, Southern Germany (*L. hortensis*: in a deciduous forest with a well developed herb layer, *L. triangularis*: in a garden with hedges).

The phenology of the two species was investigated by surveying 100–200 webs per day throughout the reproductive period. For the analysis months were divided in three parts of 10–11 days (decades).

Observations on the guarding behaviour of males were made at marked webs of subadult females which were checked at least twice a day. The time from the day of the first appearance of a male in a web to the day of the female's moult was taken as the measure for guarding duration if, on all subsequent controls, a male was present in the web. Since only few guarding males were marked individually and web-take overs were frequent this method gives no appropriate measure for the guarding duration of individual males.

Male visitation rates in webs of subadult and adult females were obtained by continuous observations (0,5–8 hours) at webs in the field (*L. hortensis*: 265 hours at 48 webs, *L. triangularis*: 387 hours at 134 webs). Male visits < 0,5 min were ignored.

In the laboratory male fights were staged in the webs of virgin females that were removed before the males were simultaneously put into these webs. The weight difference between the contestants was measured as % of the smaller male's weight.

The sperm precedence pattern was investigated in *L. hortensis* by assessing the reproductive success of sterile males in sequential copulations. Males were sterilized by X–ray or γ–radiation. A dosis of 5 Krad led to complete sterility in the males (n = 59 control copulations) without affecting the copulation behaviour. Sterile males were used only once a day. The reproductive success of second males was assessed by comparing the fertilization rates in the first three cocoons of females which had copulated successively with a sterile and a fertile male with that of females that had copulated with fertile males only.

The remating probability of females was assessed in the laboratory by testing the disposition of females to mate again with a second male after a completed first copulation. The test duration was 1–2 hours. Female behaviour during that period proved to be a reliable predictor for the subsequent behaviour.

RESULTS

Temporal availability of mating partners

The percentage of juvenile females and males during the course of the reproductive periods of both species is shown in figure 1 (data of several years pooled). In both species almost all subadult males moult considerable earlier than females. In *L. hortensis* most males mature at least 3 to 4 weeks before the females. In favourable years some males may even moult in the previous autumn and hibernate as adults. First adult males of *L. triangularis* can be found about 2 to 3 weeks earlier than adult females. In both species almost all males are adult and sexual active when the first females begin to moult.

One important difference between the two species is the length of the moulting period of the females: in *L. hortensis* moulting females can be found over a period of 6 to 7 weeks, while in *L. triangularis* almost all females moult within 3 to 4 weeks.

Male guarding behaviour

The percentage of female webs in which males are present is shown in figure 2. In both species almost all females were guarded by males at the day of their final

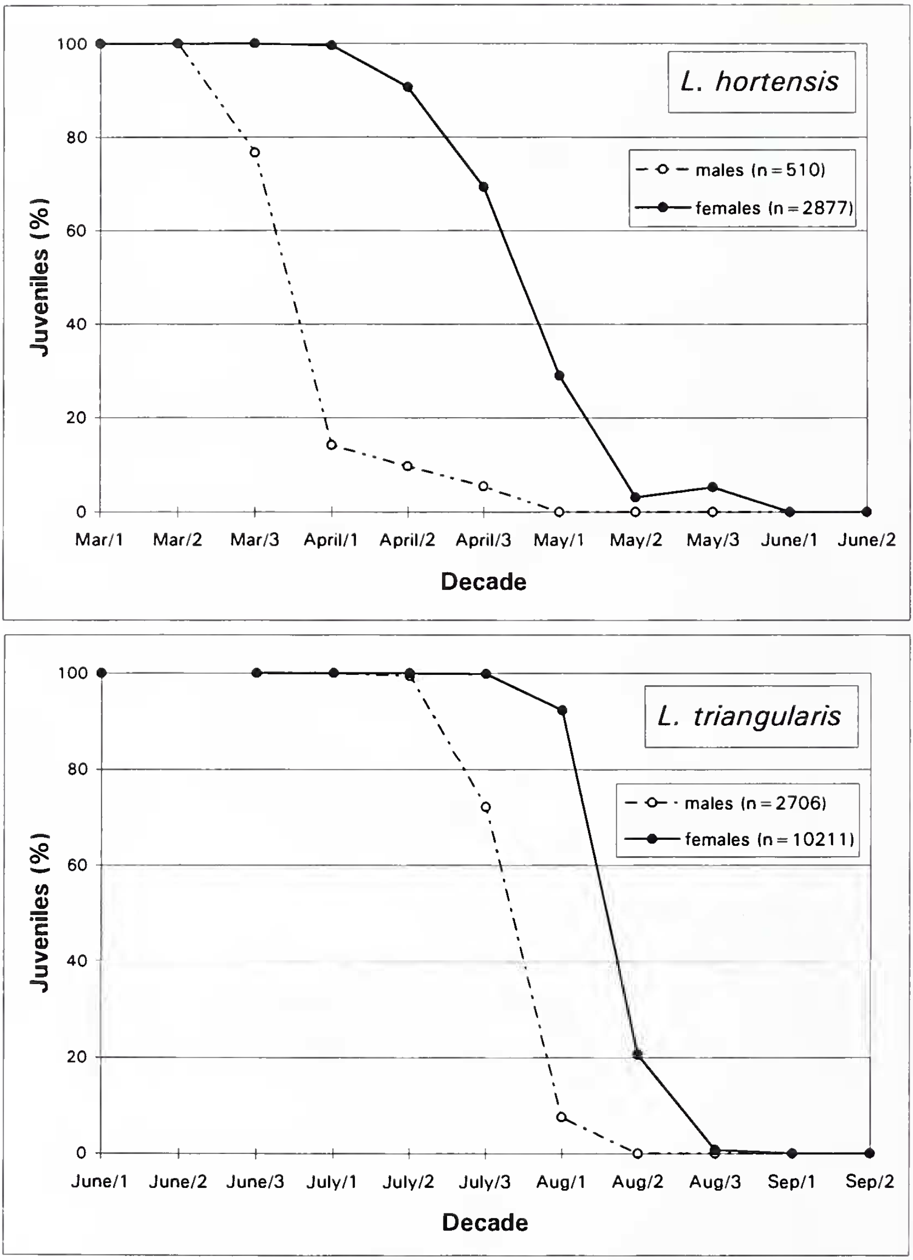

FIG. 1

Phenology of *L. hortensis* and *L. triangularis* near Würzburg, Germany: Percentage of juveniles and subadults, separated by sex (data from several years pooled, each month divided in three decades).

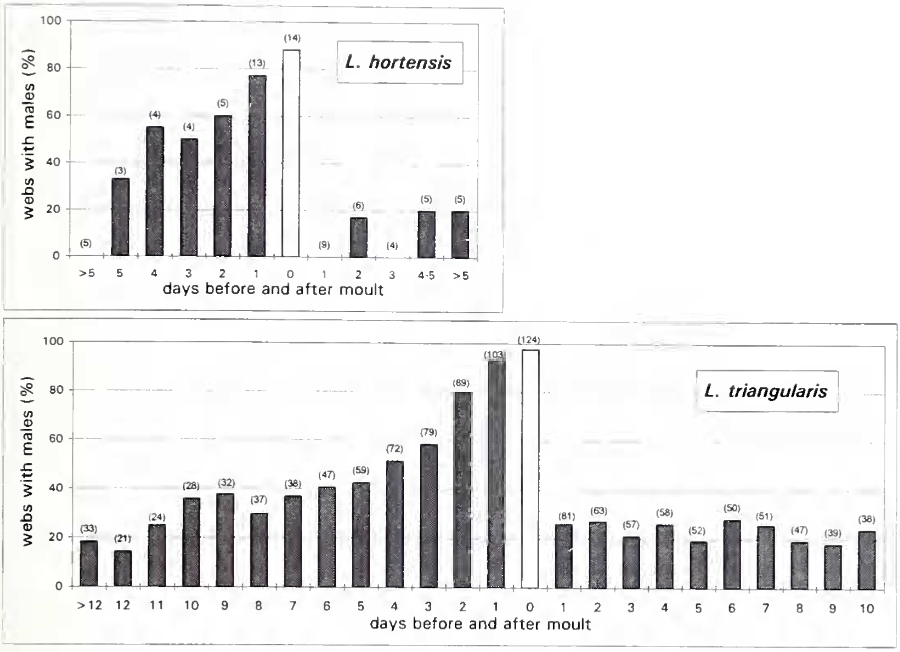

FIG. 2

Web guarding in *L. hortensis* and *L. triangularis*: Percentage of female webs with males present before and after the females' moult (day of moult = 0, sample sizes in brackets = all webs)

moult (*L. hortensis*: 88%, n = 16, *L. triangularis*: 98%, n = 124). The guarding period can extend over a considerable period, in *L. triangularis* the longest guarding duration, i.e. the period of continuous presence of males in a female's web, was 12 days and the mean guarding duration was 4 ± 2,2 days (n = 63). In *L. triangularis* where sufficiently large sample sizes are available for the whole observation period males are present only in few webs of subadult females more than 10 days before their moult. The percentage of webs with males subsequently increases continuously until the day of the moult. Copulations usually take place immediately after the females' moults (*L. triangularis*: 90% within 1 h, n = 20). After the moult the percentage of webs with males drops to a low level.

MALE FIGHTING BEHAVIOUR

Due to the observed male visitation rates in webs of subadult females of 0,2 ± 0,30 males/h in *L. hortensis* (n = 180 web hours) and of 0,1 ± 0,28 males/h in *L. triangularis* (n = 277 web hours), guarding males are often confronted with intruding males. These conflicts are usually settled in the form of intensive fights as has been

previously described for *L triangularis* by ROVNER (1968). The two species differed remarkably with respect to the duration and intensity of the fights. In *L. hortensis* the mean duration of fights (n = 68) was 10 ± 25,5 s, many fights were ended after a vibrational threat display without physical contact of the males (38%) and no male was injured during these fights. In *L. triangularis* the fights (n = 61) were considerably longer (mean duration 101 ± 170,6 s), they escalated usually to physical fighting (77% of the fights) and often males were seriously injured or even killed in these fights (15% of the fights).

COPULATORY BEHAVIOUR

In *L. hortensis* there was a considerable remating probability of females in the lab (39%, n = 340) and the mean fertilization rate of second males was about 12 ± 19,6% (n = 60, range 0–85%) of the females eggs. In *L. triangularis* the remating probability was small (10%, n = 94) and in most (8 of 9) of the few cases where a remating took place the first copulation of the females was obviously anomalous, e.g. the first male only used one pedipalpus or the intromissions of the first male were incomplete.

After a complete copulation in the copulatory openings of *L. triangularis* females a solid mass of a whitish substance is visible. This mass is firmly attached to the openings for the rest of the females lifespans.

DISCUSSION

The spatial and temporal availability of mates is a very important factor influencing the evolution of a mating system: if males and females reach adulthood at different times or with different rates the result will often be an intense competition between members of the more abundant sex (mostly males) for members of the rarer sex (ANDERSSON 1994). In both *Linyphia*-species most males are mature considerable time before the first females moult and become receptive. So even considering a presumably greater mortality of wandering males (AUSTAD 1984), at every time of the reproductive period the operational sex ratio is strongly male biased and therefore a very intensive intrasexual competition between males for receptive females is to be expected.

In most araneomorph spider species the morphology of the female spermathecae with clearly separated copulation and fertilization ducts favours sperm precedence of first males (conduit spermathecae, AUSTAD 1984): the sperm of males that copulate first should fertilize all or at least a larger part of the eggs than sperm of later copulating males. Studies of the fertilization success of second males have confirmed this sperm priority pattern in Linyphiid spiders (*Frontinella pyramitela* (AUSTAD 1982), *Linyphia litigiosa* (WATSON 1990), *Linyphia hortensis* (this study). According to this sperm usage pattern males can optimize their reproductive success by copulating with virgin females. As has been shown by JACKSON (1986) males of many spider species guard subadult females until they moult and try to copulate imme-

diately after the females' moult. In both *Linyphia*-species such a precopulatory mate guarding (PARKER 1974*a*) is the prevailing behavioural strategy males use to gain access to virgin females. Almost all of the females are guarded at the day of their moult and most of the observed copulations took place immediately after the moult. The mate guarding behaviour of *L. triangularis* has been previously investigated by TOFT (1989) in a population in Denmark where the guarding rate was lower than in the present study. So this behavioural trait may be subject to inter-population variation according to population- or site-specific factors like web density or mortality of wandering males.

In species where copulation and fertilization are separated in time and females copulate more than once there may be sperm competition between the males copulating with a female (PARKER 1970). So the number of female matings is another important variable in the mating pattern of a species. Although the mating systems of the two *Linyphia* species are very similar in some aspects they differ remarkably in others. Females of *L. hortensis* are able to mate more than once and are apparently willing to do so. Second males can fertilize at least a part of the eggs of a female in this species. Thus there is a potential for sperm competition in *L. hortensis*. By contrast, *L. triangularis* females usually mate only once and males probably avoid sperm competition by closing the copulatory openings of the females with mating plugs after the copulation which probably make these openings inaccessible to following males. In *Agelena limbata* complete plugs lead to 100% sperm priority of first males (MASUMOTO 1993). Whether the completion of the copulation or the presence of the plug is responsible for the change to avoidance behaviour in *L. triangularis*-females can not be told at the moment.

The periods during which receptive females are present in the respective population therefore differ remarkably: it is longer in *L. hortensis* where the moulting period of females is long and even females which have copulated before may remain receptive. In *L. triangularis* it is shorter because the moulting period of females is short and only virgin females are receptive.

Thus, because virgin females in *L. triangularis* are available only for a short period and because males of this species usually avoid sperm competition by sealing the copulatory openings of the females after the copulation, virgin females should be more valuable to males in *L. triangularis* than in *L. hortensis*. This different reproductive value of virgin females for males is probably responsible for the remarkably different fighting behaviour during the guarding period: males of *L. triangularis* invest more energy and take greater risks in defending subadult females against rivals than males of *L. hortensis*. The result of this inter-specific comparison agrees well with the theory of fighting behaviour by PARKER (1974*b*) who postulated that males should adjust their fighting investments to the gain that can be expected.

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